Environmental Cues and the Orientation and Movement of *Norrisia norrisii*

BY

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(2 Text figures)

INTRODUCTION

THE TROCHID SNAIL *Norrisia norrisii* (Sowerby, 1838) ranges from Point Conception, California south to Asunçion Island, central Baja California. It is found on the holdfast and stipe, and in the canopy of *Macrocystis pyrifera* (LIMBAUGH, 1955), and has been reported in the intertidal zone associated with other brown algae (RICKETTS & CALVIN, 1968).

The object of this study was to determine the movement pattern of *Norrisia norrisii* and identify the environmental cues important in maintaining the orientation that facilitates this pattern. Finally, a model is proposed based on the observations.

MATERIALS AND METHODS

Field Tests: Twenty-five *Norrisia norrisii* collected off *Macrocystis pyrifera* were measured, numbered with a yellow wax pencil, and placed on the holdfast of a 7 m *Macrocystis pyrifera* secured on a sandy bottom in 8.5 m of water. The holdfast was enclosed in a cage that prevented snails from returning to the holdfast via the sandy bottom, but allowed for free movement along the stipe. The stipe was marked every 15 cm and the positions of the snails were noted every 2 hours from 1100 hours to 2300 hours for 3 consecutive days.

Laboratory Tests: Phototaxis was tested by placing 10 *Norrisia norrisii* on the bottom of a plexiglass tank (60 × 88 × 15 cm) such that every other snail faced in the same direction. Ten minute runs were made during the day (1000 hours) and night (2200 hours) with uniform light, uniform dark, and directed light. Different snails were used for each test and mucus trails were removed after each run by washing the tank with dilute hydrochloric acid. Table 1 summarizes the experimental design and results for each test.

Geotaxis was tested in 2 series. In series A, 2 *Norrisia norrisii* were placed on a vertical plexiglass sheet, facing either up, down, right, or left. Light conditions were uniform light or uniform dark. In series B 5 snails were placed on the bottom of a plastic cylinder, 1 m high and 30 cm in diameter, under uniform light, uniform dark, or a bottom light source outside the cylinder. Each test was run for 30 minutes.

Both series were run during the day (1000 hours) and night (2200 hours). Different snails were used for each run and mucus trails were removed with dilute hydrochloric acid after each run. Table 2 summarizes the experimental design and results for each test.

RESULTS

Field Tests: The compilation of data from 3 days (Figure 1) shows a cyclic movement pattern for *Norrisia norrisii.* At mid-day (1100 hours) 58% of the snails were on the bottom third of the kelp stipe. The number increased to 65% (1500 hours), showing a general downward movement during the day. Snails on the top third of the stipe decreased in number during the afternoon (1100 - 1900 hours), while snails on the bottom third showed a continuous decrease in number after 1500 hours. At dusk there occurred a marked increase in snails on the top and a decrease in snails on the bottom. By late night (2300 hours) 51% of the snails were on the top of the stipe and 25% were on the middle.

Table 1

Phototaxic Response of *Norrisia norrisii*

Test Number	Experimental Design	Results	Number of Replicates[1]
1	Day test, uniform light	Randomly distributed with 53% at near end of tank and 47% at far end	6
2	Day test, uniform dark	Randomly distributed with 55% at near end of tank and 45% at far end	6
3	Night test, uniform light	Randomly distributed with 48% at near end of tank and 52% at far end	6
4	Night test, uniform dark	Randomly distributed with 45% at near end of tank and 55% at far end	6
5	Day test, directed light at near end of tank	93% moved toward light	6
6	Day test, directed light at far end of tank	93% moved toward light	6
7	Night test, directed light at near end of tank	78% moved toward light	6
8	Night test, directed light at far end of tank	83% moved toward light	6

[1]ten snails per replicate

Table 2

Geotaxic Response of *Norrisia norrisii*

Test Number	Experimental Design	Results	Number of Replicates[2]
Series A: vertical plexiglass sheet			
1	Day test, uniform light	100% moved up	8
2	Day test, uniform dark	50% moved up, 6% moved down, 44% were stationary	8
3	Night test, uniform light	94% moved up	8
4	Night test, uniform dark	94% moved up	8
Series B: one meter vertical cylinder (30 cm diameter)			
1	Day test, uniform light	80% at bottom, 10% at top, and 10% at middle	4
2	Day test, uniform dark	45% at bottom, 40% at top, and 15% at middle	4
3	Day test, bottom light source	85% at bottom, 5% at top, and 10% at middle	4
4	Night test, uniform light	100% at top	4
5	Night test, uniform dark	100% at top	4
6	Night test, bottom light source	85% at top, 5% at bottom, and 10% at middle	4

[2]Series A: two snails per replicate; Series B: five snails per replicate

Laboratory Tests: Phototaxic response (Table 1) to uniform light or dark during either day or night resulted in a random distribution of *Norrisia norrisii*. With directed light during the day, 93% showed positive phototaxis, while during the night approximately 80% showed positive phototaxis.

Geotaxic responses (Table 2) in series A showed that with uniform light during the day or night, *Norrisia norrisii* crawled up (94 - 100%). In uniform dark at night, the snails crawled up (94%) while during the day only 50% crawled up. In series B, during the day 80 and 85% remained on the bottom with uniform light and a bottom light source, respectively. With uniform dark, 45% remained on the bottom while 40% crawled up. Night testing under all light conditions showed *N. norrisii* crawled up.

DISCUSSION

The gross locomotor activity of *Norrisia norrisii* on *Macrocystis pyrifera* follows a circadian cycle of up during the night and down during the day. Late in the day light penetration at depth decreases; *N. norrisii* at the bottom of

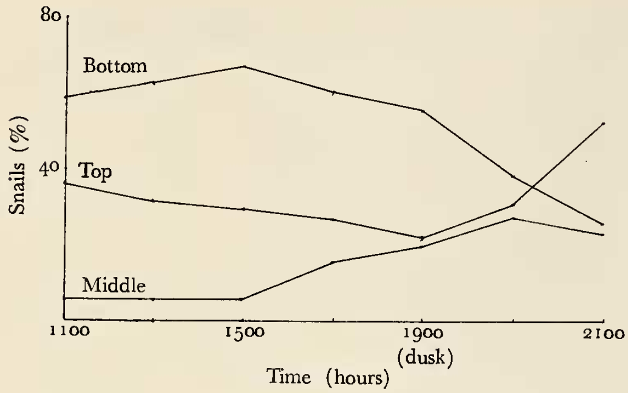

Figure 1

Movement of *Norrisia norrisii* on *Macrocystis pyrifera*

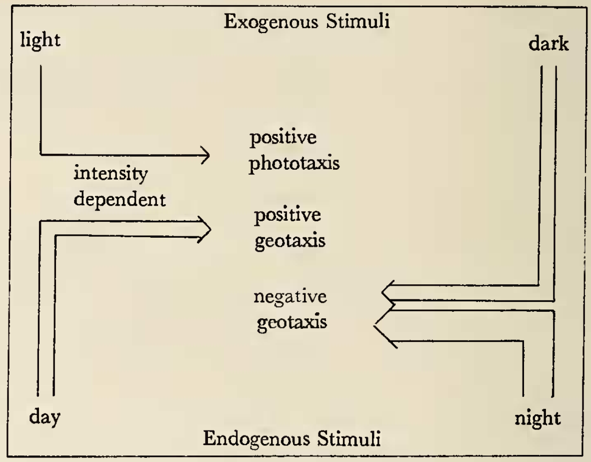

Figure 2

Model of endogenous and exogenous stimuli and responses they elicit (arrow thickness indicates relative strength of stimulus)

the kelp stipe therefore begin their upward movement earlier in the day (1500 hours) instead of at dusk (1900 hours). Snails in the middle of the stipe are indicative of the movement of snails up from the bottom and down from the top.

The presence of approximately 30% of *Norrisia norrisii* at the top of the stipe during mid-day can be explained in part by positive phototaxis. During the day or night a positive phototaxic response is elicited in the presence of a directed light stimulus (Table 1, tests 5, 6, 7, 8). Snails high up on the kelp stipe may be temporarily "trapped" by this phototaxic response, delaying their downward movement till late afternoon. The strength of the phototaxic response may depend on light intensity, decreasing as the intensity decreases. It is known that light intensity has a profound effect on activity level and the ratio of activity to resting (Marler & Hamilton, 1966). The shadowing effect of the cove in which the field tests were run may have delayed positive geotaxis until the sun reached a relatively high (and therefore intense) position in the sky, resulting in positive phototaxis and entrapment. Late in the afternoon positive phototaxis decreased as light intensity decreased, resulting in the observed positive geotaxis.

A model of endogenous (day, night) and exogenous (light, dark) stimuli eliciting geotaxic and phototaxic responses is presented in Figure 2. The model is hypothetical and attempts to account for the movement pattern of *Norrisia norrisii*.

Gravity, as a stimulus, differs from light in that it cannot vary in intensity or direction and therefore cannot be tested as two differentially arranged stimuli (Fraenkel & Gunn, 1940). The geotaxic response of *Norrisia norrisii* to gravity is mediated by the exogenous dark stimulus and the endogenous day-night stimuli. It is probable that these mediators reach a threshold level which releases an all-or-nothing geotaxic response to the gravity stimulus.

The model is based on geotaxic responses (Table 2) and field observations (Figure 1). The only significant discrepancy between the model and the data is test 1 of series A where an endogenous day stimulus resulted in negative geotaxis. Reexamination of technique showed that *Norrisia norrisii* was subjected to extreme handling stress in series A and it is possible that an escape response may, in part, account for the discrepancies in the results. Snails in series B were minimally handled and allowed to respond in undisturbed conditions.

CONCLUSIONS

The movement pattern of *Norrisia norrisii* on *Macrocystis pyrifera* is facilitated by the manner in which it orients to exogenous and endogenous stimuli. A hypothetical model based on field and laboratory tests presents a possible mechanism of orientation and movement. The endogenous night stimulus is dominant and serves to trigger negative geotaxis. Endogenous day and exogenous dark stimuli are of equal strength and trigger positive and negative geotaxis respectively. The exogenous light stimulus triggers positive phototaxis and the degree of response may be dependent on the intensity of the light stimulus.

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